BIOGEOGRAPHY AND ORIGIN OF SOLANUM ACAULE BITTER

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The wild Andean potato species, S. acaule Bitter, has long been of interest to both the systematist and the horticulturalist because of its tetraploid chromosome number (2n=48; an amphidiploid fide Rybin 1929, 1933), and the fact that it grows at high elevations under climatic conditions which are unsuited for the cultivation of the common potato, S. tuberosum L. As this species is remarkably resistant to frost, it has been utilized by plant breeders in the development of several new varieties of the cultivated potato which are adapted for growth in northern regions.

However, the botanical origin of S. acaule, as well as its reproductive behavior and biogeography, remain as several aspects of its natural history which have not as yet been sufficiently explored, and which are in need of further study if the full potential of this species for varietal improvement purposes is to be realized. It is towards the partial fulfillment of these ends, therefore, that the following remarks have been directed.

ECO-GEOGRAPHIC CONSIDERATIONS.--S. acaule is a low, rosette-forming plant of the Peruvian-Bolivian altiplano and high mountain regions of northern Argentina. It is usually found between 3500 and 4500 meters, although individuals growing just below snow line at elevations of 5000 meters have been reported (Bukasov 1939). It occurs at elevations higher than that known for any other potato species. Its north-south extension is about 2700 km., occurring from the Department of Cajamarca, Peru, to the Andes of La Rioja, Argentina (Fig. 1).

As in the case of the many wild diploid species of Solanum, Section Tuberarium (cf. Correll 1962), which grow primarily in weedy or disturbed habitats throughout the Andes, the tetraploid S. acaule also grows along open roadsides, trails, and cultivated fields, as well as in and along the rock rubble of ancient Inca ruins. The natural habitats of this plant, however, are in the seasonally dry and windswept grasslands (or punas) of southern Peru and northern Bolivia. These high tableland communities are essentially devoid of the thorny bushes, large cacti, cliffs, rocks, and other natural features which, in other places, often serve to shelter and protect the wild species of this group from grazing animals. However, S. acaule not only tolerates but seems to prosper under conditions of

Fig. 1. Distribution of Solanum acaule.

heavy grazing. This behavior, an oddity in Section
Tuberarium, is also shared by S. megistacrolobum, a
rosette-forming diploid species with which it sometimes
grows.
        Plants of S. acaule are frequently found growing
between clumps of Stipa ichu Kunth, one of the wire-
leaved species of bunch grasses which are so common in
the Andes. The spaces between these tussocks are
frequently heavily grazed by llamas and alpacas, or by
sheep, horses or cattle. And yet, little harm appears
to be done to these plants by animals. Since the leaves
of S. acaule are spread flat upon the ground, forming a
rosette, they are cropped only with difficulty by the
grazing animals (compare, in this case, the common dande-
loin, Taraxacum officinale Weber, a rosette-forming
species notorious for its resistance to mowing).
Similarly, the flowers, while occasionally grazed, are
largely protected by their proximity to ground level.
The stems and fruiting pedicels of this species, however,
commonly elongate greatly at maturity, thus elevating
the berries to a height where they can be more readily
cropped by grazing animals.
        The ability of this species to grow and prosper
under conditions of heavy grazing would appear to be
related to both its growth form and to its manner of
seed dispersal. Abundant individuals of this species,
for example, are commonly to be found in the vicinity of
shephard's huts (chozas) in the high Andes, as well as
in the compacted, rocky soils of nearby fields and
yards where sheep, llamas, and alpacas are herded for
the night. The soil in these areas is covered with a
layer of animal droppings, these usually containing the
undigested and still viable seeds of a number of different
plant species, including S. acaule. Later, when the seeds
germinate, the rotting manure provides abundant fertilizer
for the developing plantlets.
        It is apparently not unusual for the seeds of certain
plant species to be distributed in this manner. Rick
(1961), for example, reports that the seeds of certain
Galapagos varieties of the common tomato (Lycopersicon
esculentum var. minor) are regularly dispersed from
island to island as a result of the migratory wanderings
of the giant tortoise, Testudo elephantopus porteri. The
results of germination tests conducted on the seed
recovered from the feces of these animals suggest that the
mild digestive treatment they receive is an important
factor in the breakage of the seed dormancy of these
varieties. Without such treatment, less than 1% of the
seeds of the tomato will germinate naturally, as opposed
to 85% of seeds obtained from fecal matter.
        Similar germination test-results have been reported
by Harman and Keim (1934) for the seed of six different

species of weeds recovered from the manure of calves, horses, sheep, hogs and chickens; by Burton and Andrews (1948) for the seed of Bermuda grass fed to cattle; by Roessler (1936) for the seed of certain weed species digested by California linnets or finches; by H.G. Baker (in Rick 1961) for the seed of the African baobab and sausage trees collected from the dung of baboons; and by Rick (1961) for the seed of edible species of Carica and Passiflora eaten by human field workers in Ecuador!

Another line of evidence relating to the dispersal of the seed of S. acaule by means of grazing animals concerns the fruiting pedicels of this species. These, unlike those of any other species of this section, are non-articulated. Thus, the fruits normally remain firmly attached to the stem until they are cropped by grazing animals, and are not easily dislodged by birds, wind, or rain. This then, along with the factors related above, would tend to explain the frequent occurrence of this plant along roadsides, pathways, adobe walls, fields and water courses, as well as in village courtyards, plazas, and other places where grazing animals are occasionally herded.

The llama, which is the common beast of burden in the high-lands of Peru and Bolivia, is mostly driven at a leisurely pace, in a herd, grazing as he goes. The seed and fruits of the plants that are eaten at the start of a journey, or along the way, may thus be contained in droppings spread along a 15 to 25 kilometer path by nightfall. As pointed out previously, the germinability of seed distributed in this manner is much improved as the result of the scarification of the seed coat through the action of intestinal enzymes and stomach acid.

Grazing animals, as seed dispersal agents, may occasion-ally introduce two or more closely related species into an open habitat where, if conditions are favorable, they hybridize. The Argentine triploid, S. brucheri Correll (2n=36), appears to have been formed in this manner. According to Brücher (1959), it is a naturally occurring hybrid between S. acaule (2n=48) and S. megistacrolobum (2n=24). Correll (1962) remarks that this plant frequently grows in dung deposited in the places where grazing animals congregate for the night. He cites specimens collected from sheep corrals, and from roadsides, rockwalls and yards of livestock ranches. Solanum acaule and S. megistacrolobum are also found in these same habitats and have been cited as occurring in the same localities as S. brucheri by Correll and Brücher (1959). These observations suggest that grazing animals may play a much more important role in the evolution of diverse new forms of Solanum than has been previously thought.

BREEDING BEHAVIOR.--In contrast to the wild diploid potato species of Peru, Bolivia, and Argentina, all of which are self-sterile and are thus obligate outcrossers, the tetraploid S. acaule is self-fertile and in the greenhouse, at least, self-pollinated. Self pollination in this species is facilitated by

the short non-exerted style and the spacial proximity of the
stigma to the anther pores, as well as by the occasional develop-
ment of cleistogamous flowers.

Although little is known with regard to the physiological
mechanisms which underlie cleistogamy, certain environmental con-
ditions would appear to favor this mode of reproduction. Thus,
according to Davis and Heywood (1963), cleistogamy is of more
frequent occurrence in plants which grow in high mountain regions
as well as in the far north or far southerly reaches of the
world. It is also common at low elevations in plants which have
been exposed to prolonged wet weather, drought, cold, heat or
deep shade, all conditions associated with a scarcity of insect
pollinators. Cleistogamy may function as an aid in the survival
of the species in such situations, and especially in cases where
normal means of cross-pollination would be prevented.

The ability of S. acaule to thrive on the cold, seasonally
dry high-altitude grasslands of Peru and Bolivia may be partly
due to its predominantly autogamous breeding system, a condition
which permits the development of many-seeded berries on plants
which would otherwise have few or no insect pollinators, and
hence few if any fertile, seed-containing fruits. In evolutionary
terms, autogamy may be seen as important in that it favors the
formation of genetically homozygous populations. A lack of
variability may be advantageous in a uniform environment, as it
permits a successful biotype to rapidly colonize its local area.
Once a particularly well-adapted biotype of this species has
become established, it is capable of maintaining its identity by
means of seed obtained through selfing, as well as through
vegetative means (i.e., propagation by stolon and tuber forma-
tion).

The breeding behavior of the diploid and obligate-outcrossing
species most closely related to S. acaule, namely S. canasense,
S. brevicaule, and S. megistacrolobum, contrasts markedly with
that of this species. Although outcrossings within diploid popu-
lations may often result in a swarm of genotypically heterozygous
seedlings, only few of these may be expected to be well-adapted
to any particular habitat, or environment. This type of breeding
system, of course, may be advantageous under certain ecological
conditions, for it allows the species to adapt itself to changing
environments or to colonize a diversity of habitats. Once
successful genotypes are established, they may persist for many
generations in a particular habitat through a combination of
seed and vegetative reproduction. Thus, the diploid species
exhibit much flexibility in breeding behavior. Significantly, it
is this adaptability which promotes the formation of hybrid
swarms between S. megistacrolobum and S. canasense in Peru and
the former species and S. brevicaule (a close relative of
S. canasense) in Bolivia. As pointed out elsewhere, these hybrid
swarms frequently contain diploid segregates that are markedly
similar in flower, leaf, and habit to S. acaule (cf. Ugent 1970-A).

CROSSABILITY OF S. ACAULE.--Two frost resistant cultivars grown in the Lake Titicaca region of Peru and Bolivia are known to be naturally occurring hybrids of S. acaule and S. tuberosum. According to Hawkes (1962), S. x juzepczukii (2n=36) is formed in crosses between S. acaule and S. tuberosum Group Stenotomum (2n=24), while S. x curtilobum (2n=60) arose from crosses between S. x juzepczukii and S. tuberosum Group Andigena (2n=48).

Although the above hybrids are partially sterile, intro-gression can often take place against strong reproductive barriers, as, for example, in the case of S. x edinense and the cultivated potatoes of Mexico (Ugent 1967), and various species of Tradescantia (Anderson & Hubricht 1938), Helianthus (Heiser 1951), and Aegilops (Pazy & Zohary 1965). Natural gene exchange between the hybrids of S. acaule and the cultivated potato popu-lations of the Lake Titicaca basin may thus be responsible not only for the great variability of the cultivars grown in this region, but for their generally high frost tolerance as well.

As mentioned earlier, the Argentine triploid, S. brucheri, is formed in natural crosses of S. acaule with S. megistacrolo-bum (see Hawkes 1963, 1969). S. acaule has also been experi-mentally crossed with S. megistacrolobum, and with the two other species of concern to this study, S. canasense and S. brevi-caule (Ross & Rowe 1972; Okada 1973; Hawkes 1969). Other species within its natural area which it also has been experimentally crossed with include S. sanctae-rosae, S. sparsipilum, S. kurtzi-anum, S. tarijense, S. infundibuliforme, S. multidissectum and S. sogarandinum. In addition, S. acaule has also been artifi-cially crossed with the following species, none of which, however, are found within its natural range: S. bulbocastanum, S. cardio-phyllum, S. pinnatisectum, S. maglia, and S. chacoense.

According to Hawkes (1969), some of the specimens cited by Correll (1962) as collections of S. brucheri may be mis-identified. These he has referred to as naturally occurring hybrids of S. acaule and S. infundibuliforme. Also, Hawkes reports the species S. acaule hybridizes naturally with S. megistacrolobum and S. spegazzinii in Argentina. Thus, on the whole it would appear that the plants of this section are all very closely related, and that differences in chromosome number are only a minor obstacle to further speciation.

As in the case of other polyploid pillar complexes (cf. Davis & Heywood 1963), crossing can take place here, at and between the various levels of ploidy, and the spontaneous doubling of the chromosome number of diploid hybrid forms is not totally unknown. Since S. acaule lacks close relatives at the tetraploid level, we must look toward the diploid species, notably S. canasense, S. brevicaule, S. megistacrolobum, and their hybrid segregates, for a possible origin.

VARIABILITY OF S. ACAULE.--The mature terminal leaflets of S. acaule are amongst the smallest of any known potato species, and are usually less than 5 cm long and 4 cm wide, and sometimes

as little as 0.5 cm long and 0.5 cm wide (Fig. 2). The size
relationships between the terminal leaflets of tetraploid popu-
lations of S. acaule and diploid populations of S. canasense,
S. brevicaule and S. megistacrolobum have been illustrated
elsewhere (Ugent 1966). While some differences are found in
the shape of the terminal leaflet of S. acaule, the general
tendency is toward a broadly ovate-elliptic or suborbical leaf-
let, much as occurs in hybrid diploid segregates of these taxa
(Ugent 1970-A). The extreme sub-orbicular terminal leaflet
condition of S. acaule may be employed as a useful character in
distinguishing this species from similar appearing rosettes of
S. megistacrolobum.
       Populations of S. acaule vary considerably in pubescense,
length and width of terminal leaflets, number of interjected
leaflets and leaf length (Fig. 2). However, the low rosette
habit, greatly abbreviated stem and peduncle, and the peculiar
non-articulated pedicels (the place of articulation marked only
by a ring of purple pigment) are features of this amphidiploid
that are relatively constant. These features, plus the distinct
chromosome number of S. acaule, induced the Russian taxonomists,
Juzepczuk and Bukasov (1937), to segregate this single species
as the series Acaulia of Sect. Tuberarium, a classification
subsequently maintained by Hawkes (1944, 1956, 1963), Correll
(1962) and Ochoa (1962).
       Various populations of S. acaule vary in leaflet number
from 5-13, with a mode of 9. The leaves of cultivated material
of this species are distinctly more dissected, varying from 9 to
15 leaflets, with a mode of 13. A study of the scatter-diagrams
in Fig. 2 also reveals that the leaves of cultivated material
tend to be longer than wild plants, with narrower terminal leaf-
lets and longer lateral leaflets. Noticeable variation is also
found between wild and cultivated material with respect to the
frequency of interjected leaflets. Although wild plants gen-
erally lack interjected leaflets, there may occasionally be 1 or
2, and rarely as many as 11. Cultivated material frequently has
4-10 interjected leaflets and occasionally as many as 17. It is
of interest to note that the leaves of the closely related
species, S. canasense and S. brevicaule, though generally more
dissected than S. acaule, show nevertheless the same tendency
for increased dissection under cultivation.
       ORIGIN OF S. ACAULE.--The manner in which this species
arose has long been a matter of conjecture. Both Hawkes (1947,
1963, 1969) and Correll (1962) believe this species to be the
South American phytogeographic equivalent of S. demissum, a
rosette-forming hexaploid (2n=72) of central Mexico and Guate-
mala. However, it is highly doubtful whether these species have
had a true vicarious origin or whether they are even distantly
related. The two species differ in a number of important
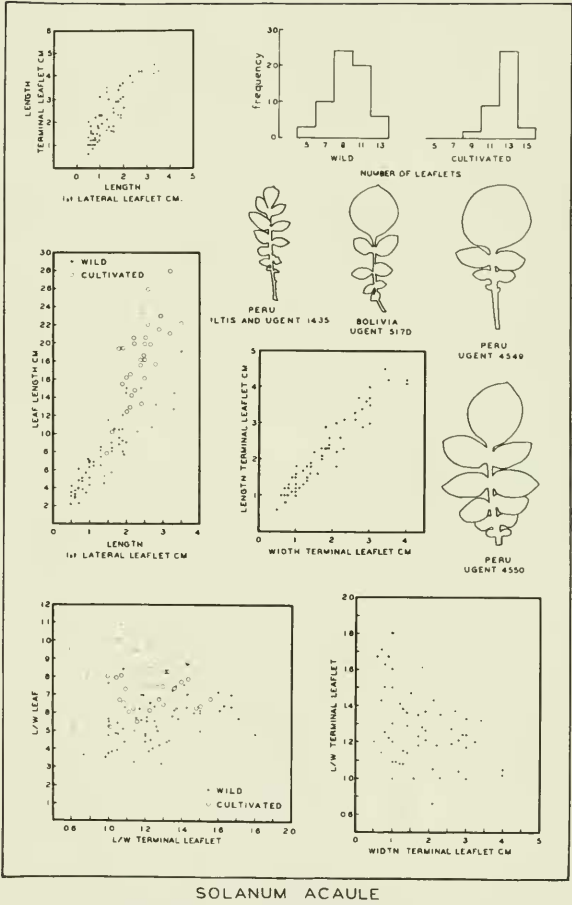morphological characters, have rather dissimilar patterns of

Fig. 2.   Morphological variation in <u>Solanum</u> <u>acaule</u>.

variability, and do not seem to be closely allied either geneti-
cally or ecologically. The reason that authors concluded a
relationship can be found in the rosette habit, small stature,
and rotate flowers. However, the first two of these characteris-
tics appear to be brought about by convergence. Löve (1954)
advocates the use of the term "false vicariads," or "substitu-
tion taxa," to describe fully allopatric taxa, such as these,
that are heteroploid, of independent origin, and only of super-
ficial morphological similarity.

Bukasov (1960) suggests that series Acaulia is of recent
polyploid origin and has evolved from South American diploid
species. His conception of the phylogenetic affinities of the
various potato series is given diagramatically in the form of a
"phylogenetic tree" based upon ploidy level, geography and
morphology. In his diagram we find series Acaulia and series
Megistacroloba diverging from a common point on or about the
center of an "Andean group" branchlet. This radiates in turn
from a forked stem bearing the label "South American branch."
The various branches and branchlets are ultimately joined to a
common base or stem, thus signifying the monphyletic origin for
Sect. Tuberarium.

Bukasov's basic premise, Sect. Tuberarium as a natural
group, can be here agreed to only with the revisions proposed by
the present author in another study, especially in regard to the
placement of the species in series Juglandifolia (see Ugent
1966). Nevertheless, one can not but agree that series Acaulia
is closely related to series Megistacroloba, and especially to
the type species S. megistacrolobum, the latter also a rosette-
forming species and one which has similar distribution and
habitat preferences as S. acaule. However, the maximum correla-
tion of acaule-like characters are to be found in plants
derived from natural crosses of S. megistacrolobum with S. cana-
sense, or S. megistacrolobum with S. brevicaule.

Hybrid swarms between S. megistacrolobum and S. canasense or
the very closely related (if not conspecific) S. brevicaule
nearly always contain segregate forms that are remarkably similar
to S. acaule in their acaulescent rosette habit, leaf shape and
dissection, and broadly rotate flowers. These forms often differ
from S. acaule only by being diploid, self-sterile, and in
having articulated pedicels and slightly larger flowers.

From the study of such hybrid swarms it is suggested here
that S. acaule may have originated in a complex multi-step
process involving: a) hybridization between S. megistacrolobum
and one or the other (or both) of the two species mentioned
above; b) segregation of acaule-like forms; c) doubling of the
chromosome number; and, d) differentiation as the result of
genetic isolation, self-fertility, inbreeding and natural selec-
tion (cf. Ugent 1970-B).

Grazing animals probably facilitate the establishment of
hybrid swarms between S. megistacrolobum and S. canasense in Peru
or S. brevicaule in Bolivia by introducing their seed into dis-

turbed or artificial habitats. The variant forms which develop
in these open habitats may be subject not only to the selective
whims of their respective physical environments, but to the
selective pressure of the grazing animals which aided in their
original establishment as well.

Thus, in areas of intense grazing pressure, hybrid segre-
gates with low rosette forms may persist by clonal propagation
for an indefinite number of generations, and may accumulate in
yearly numbers through repeated hybridizations and selections.
In each successive generation there exists a possibility for the
chance formation and fusion of two unreduced gametes, or amphi-
diploidy.

Once acquired, amphidiploidy may bring about rapid stabili-
zation of acaule-like characteristics, especially as this condi-
tion often results in increased self-fertility, inbreeding and
genetic isolation from diploid populations.

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